Bacteria and Archaea in the Marine Environment

EBS 566

Reading

- Chapter 5, Miller
- Discussion paper:
  - Martens-Habbena et al. Ammonia oxidation kinetics determine niche separation of nitrifying Archaea and Bacteria. Nature (2009) vol. 461 (7266) pp. 976-979

A Microbial World

- "The most outstanding feature of life's history is that through 3.5 billion years this has remained, really, a bacterial [microbial] planet. Most creatures are what they've always been: They're bacteria [and archaea] and they rule the world. And we need to be nice to them."
  - From: "Stephen Jay Gould" (Interview by Michael Krasny). Mother Jones (Jan.-Feb. 1997): 60-63. ©1997
- See also the essay “Planet of the Bacteria”
  - http://www.stephenjaygould.org/library/gould_bacteria.html

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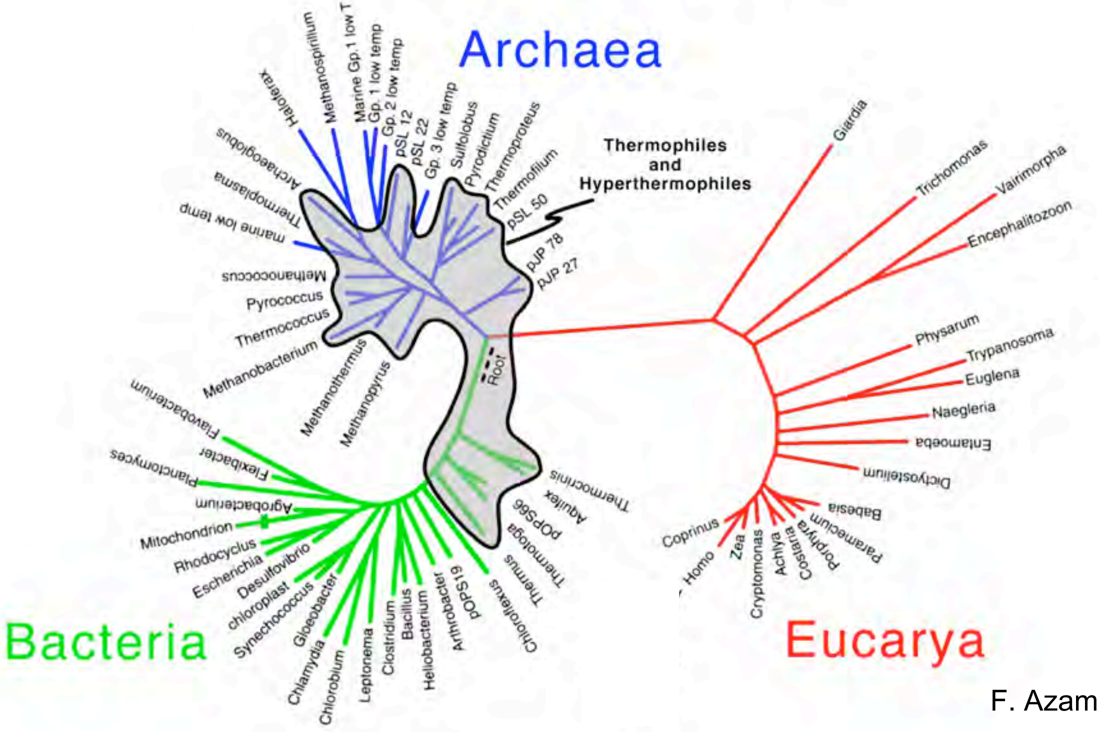
What are microbes?

- Too small to perceive individually
  - Microscopy is central
- Often single cells
- Bacteria
- Archaea
- Small Eukarya
- For this lecture we’ll include viruses, which are not cells, but are part of the microbial community

The Tree of Life

Most marine biodiversity is microbial



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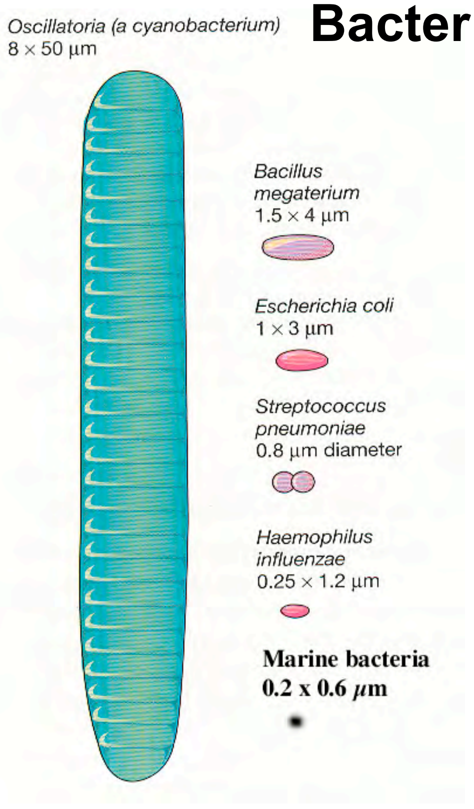
Bacteria Size (small!)



- **Typically 0.5 - 2 µm**
- ***E. coli* volume is ~ 1 μm^3**
- **Pelagic marine bacteria *in situ* ~ 0.03 - 0.07 μm^3**
- **Giant: Surgeonfish symbiont *Epulopiscium fishelsoni*; 600 µm rod**
- **Many small ones can enlarge**

Consequences of being so small:

- **Large surface area to volume ratio**
- **Limits space for DNA, ribosomes, etc.**

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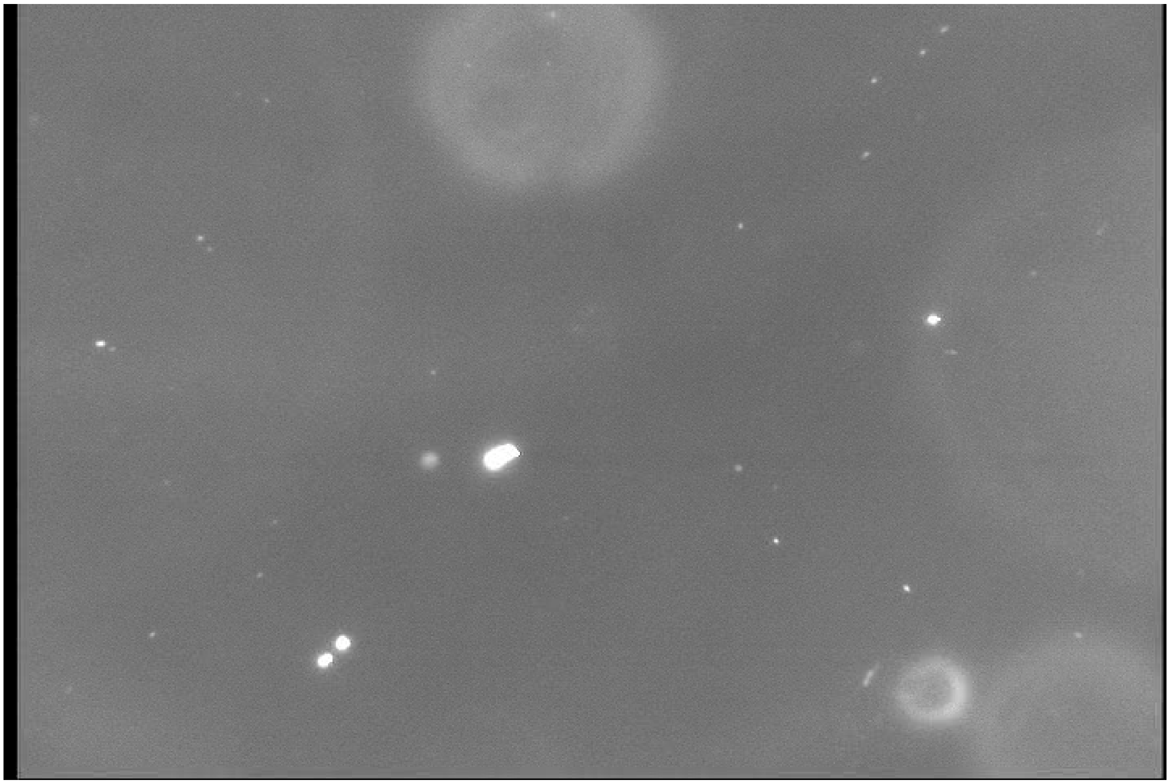
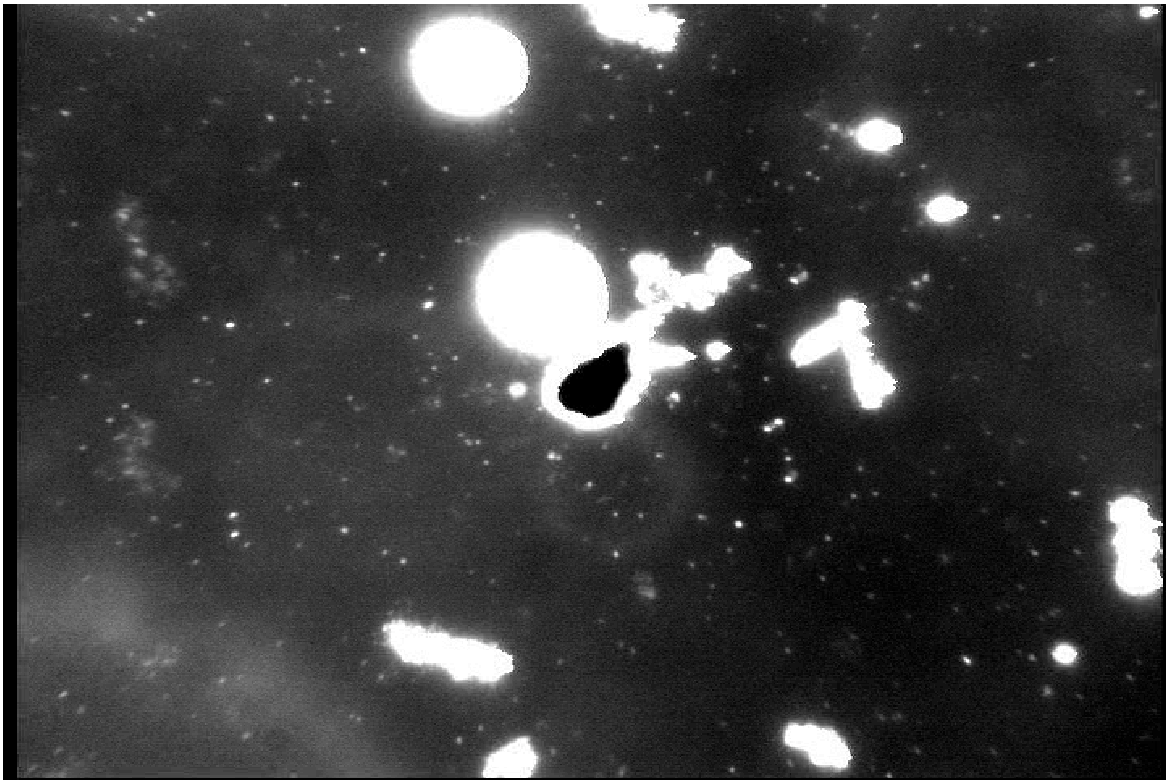
A drop of seawater

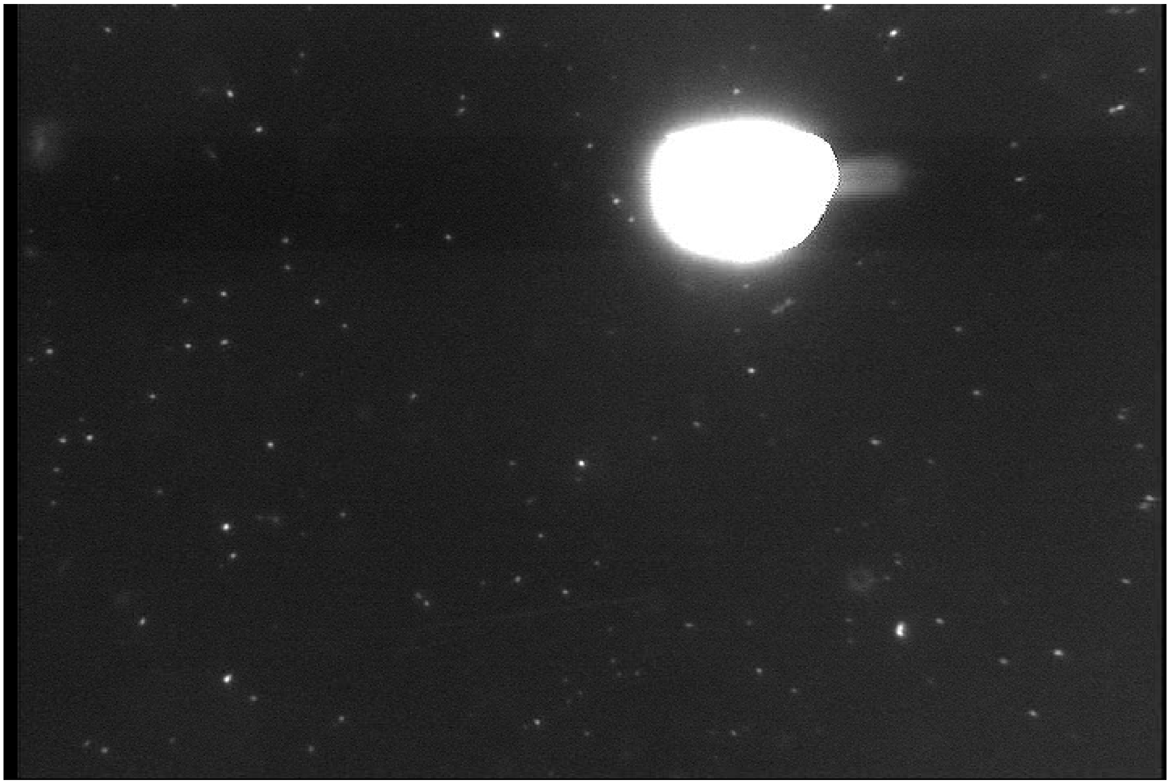
- By Farooq Azam, Professor, Scripps Institution of Oceanography



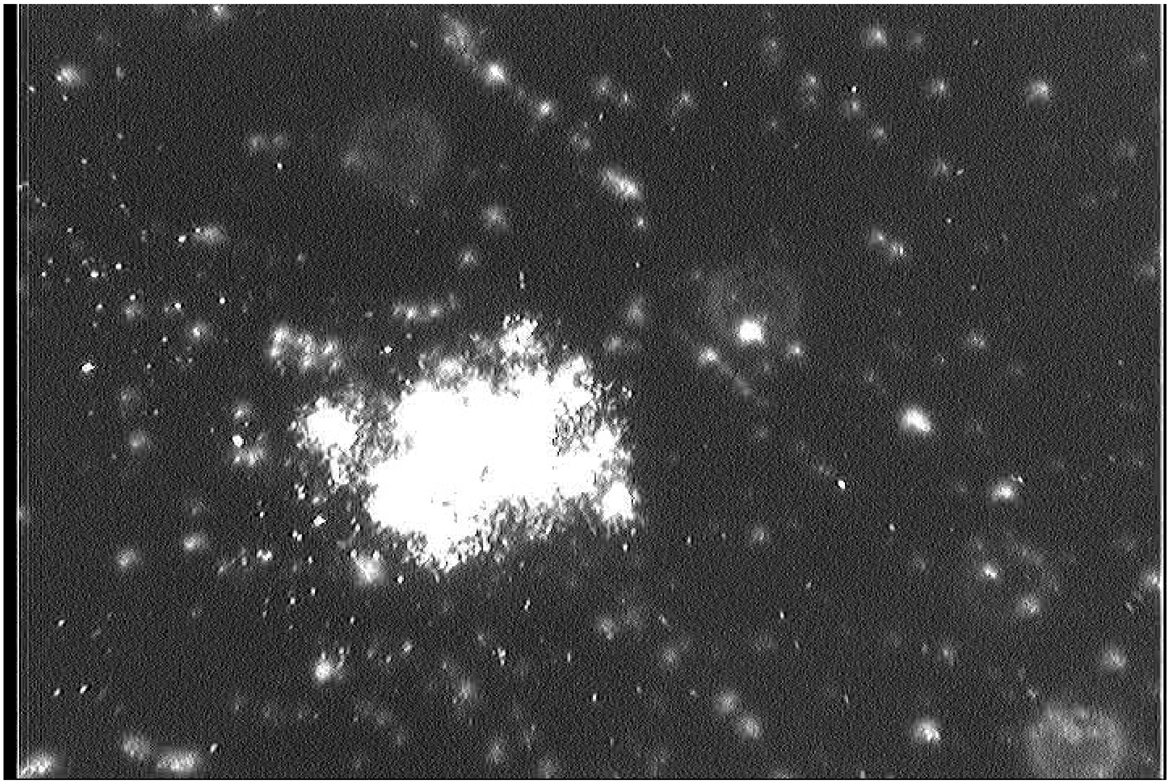
A drop of seawater from Scripps pier, dark field microscopy (100x magnification)



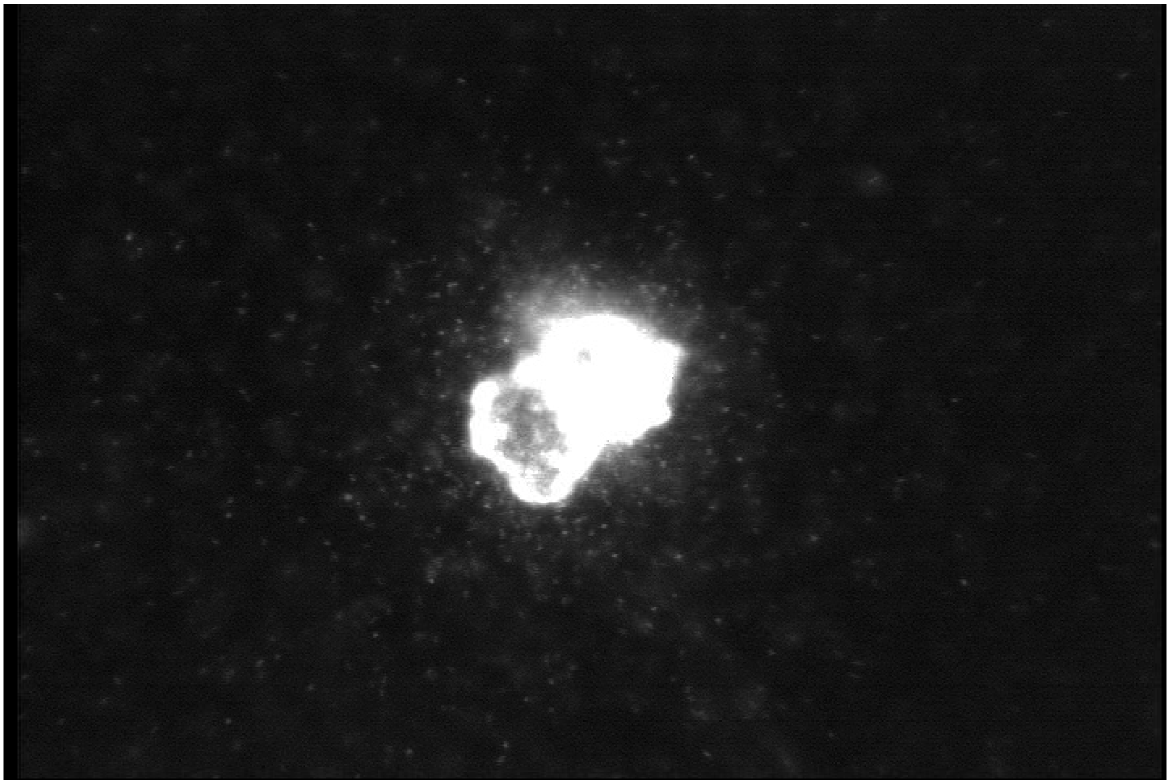
A drop of seawater enriched with particles, dark field microscopy (100x magnification)



Seawater bacteria with a cell of the red tide dinoflagellate *Lingulodinium polyedrum*



Seawater bacteria near a piece of detritus, dark field microscopy (100x magnification)

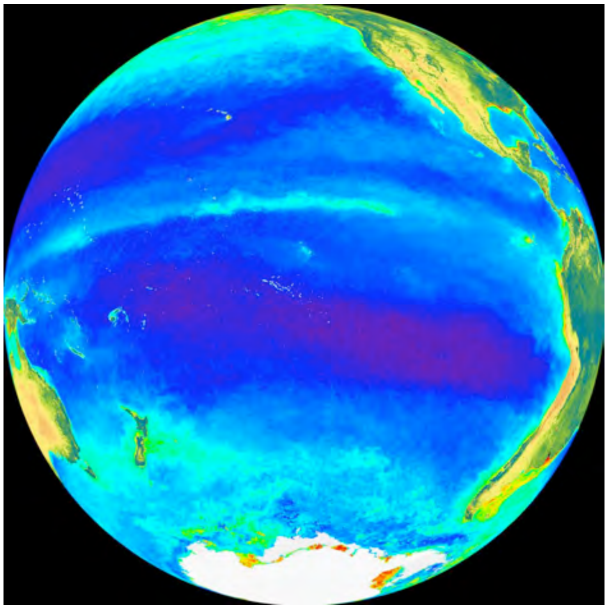


Vibrio cholerae culture clustering around a dead dinoflagellate

What is the ocean?

- What are the properties that shape the evolution of marine microbes?

OCEAN AS A MICROBIAL HABITAT



http://seawifs.gsfc.nasa.gov

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Effect of temperature on growth

- Skewed growth rate vs. temp curve very similar to enzyme activity curves
- Temperature curve affected by growth medium/conditions

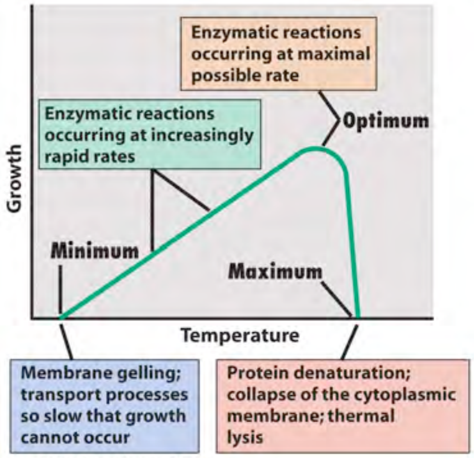

Figure 6-16 Brock Biology of Microorganisms 11/e
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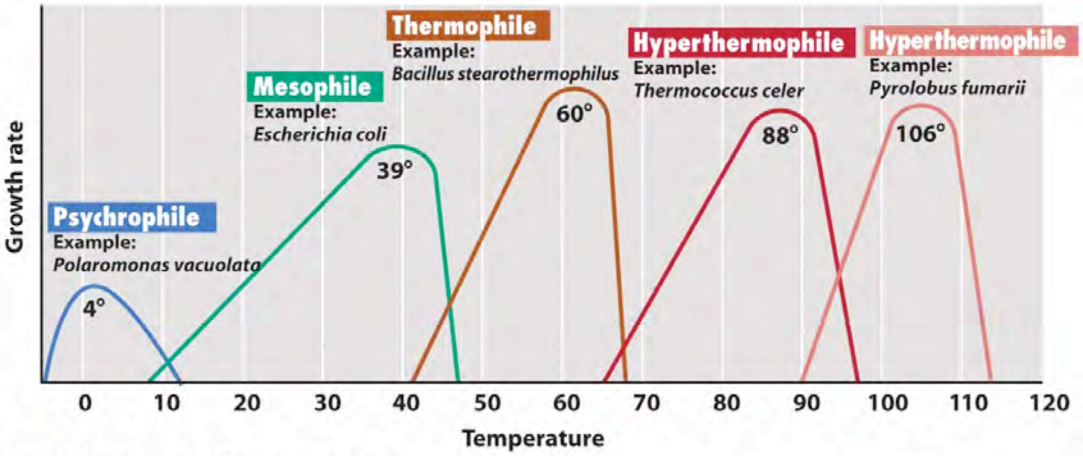
Temperature terminology



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From: *Marine Biology: Function, Biodiversity, Ecology* (2nd Ed., 2001) by Jeffrey S. Levinton

Temperature profile

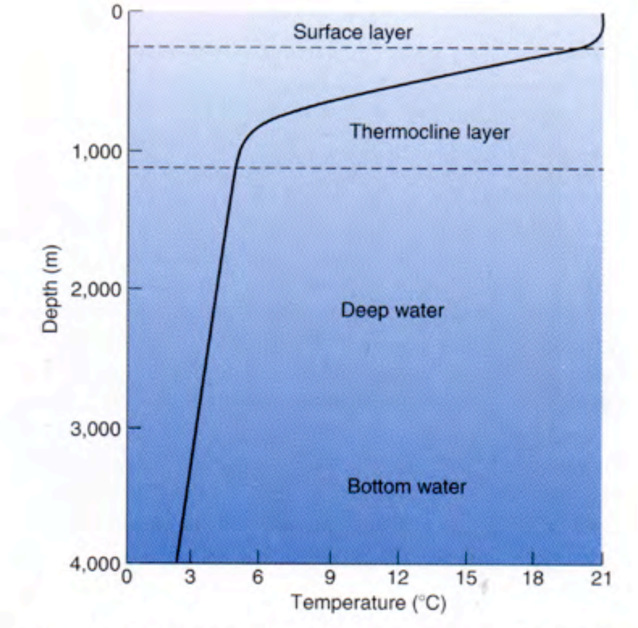
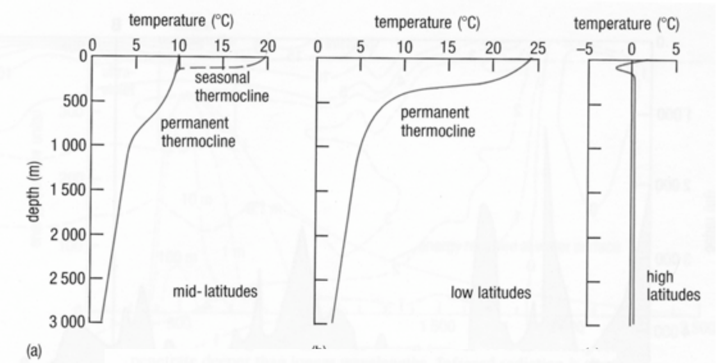
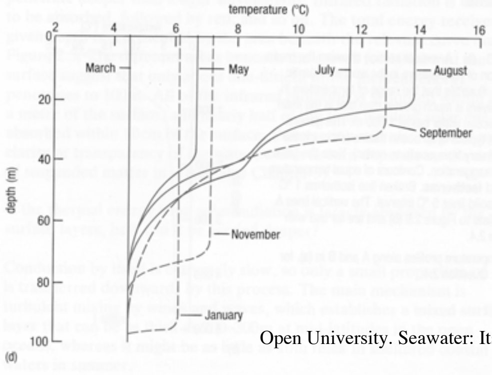


Fig. 2.15 An idealized profile of seawater temperature as a function of depth.

Temperature as a Variable





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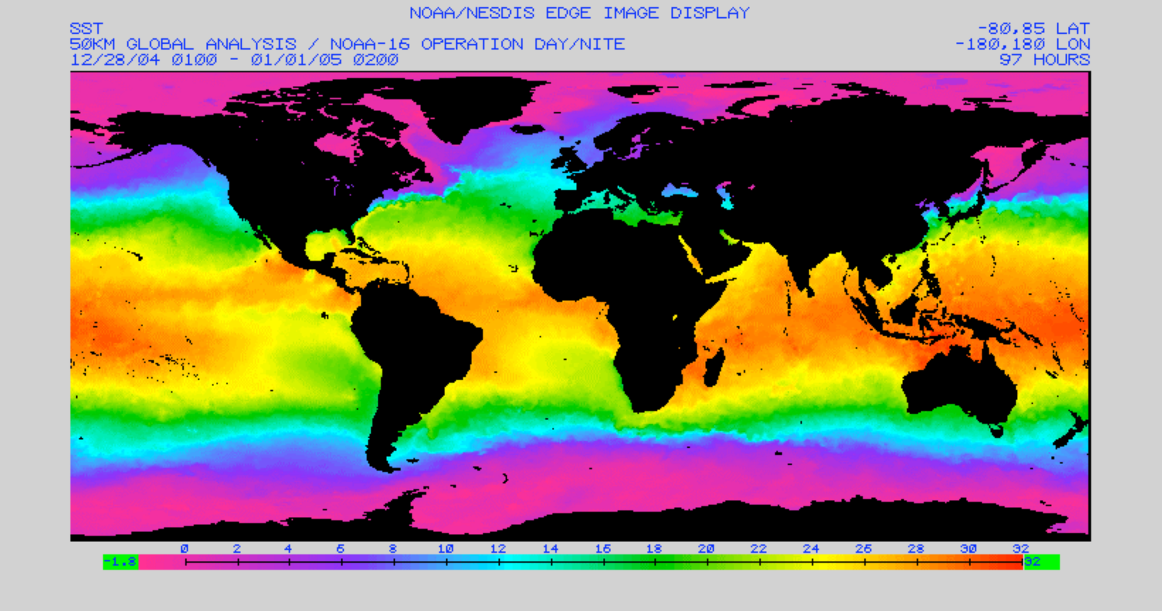
Open University. Seawater: Its composition, Properties and Behavior. 1991.

Sea Surface Temperatures

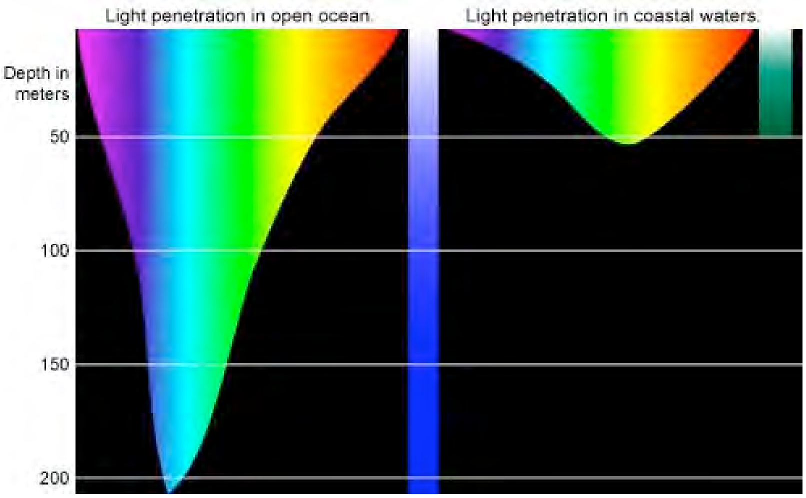


http://www.osdpd.noaa.gov/PSB/EPS/SST/data/FS_km5000.gif

Temperature

- Most marine microbes are adapted to lower temperatures than microbiologists are used to

Light as a variable



http://oceanexplorer.noaa.gov

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Light

- Critical variable for phototrophs
- Low and high light level adaptations (e.g. *Synechococcus* and *Prochlorococcus* ecotypes)
- UV damage potential in upper layers
- DOM transformation by UV-- indirect effect on bacterial growth

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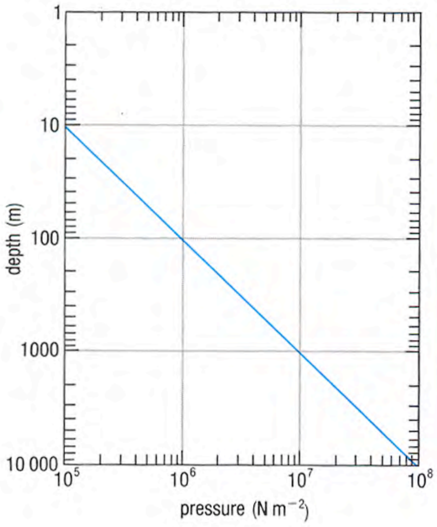
Pressure as a Variable



Piezophiles

Open University. Seawater: Its composition, Properties and Behavior. 1991.

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Pressure

- 1 atm/10 m depth
- Most ocean volume below 1000 m
- Adaptations for piezophily (enzyme expression)
- Challenge for surface bacteria sinking w/particles- implications for OM decomposition
- Challenge for bacteria rising with light particles

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Major ions – Seawater vs. River Water

Ion	Average Seawater (mM)	Average River (mM)
Cl^-	545.0	0.16
Na^+	468.0	0.23
Mg^{2+}	53.2	0.15
SO_4^{2-}	28.2	0.86
Ca^{2+}	10.2	0.33
K^+	10.2	0.03

From: *Marine Biology: Function, Biodiversity, Ecology* (2nd Ed., 2001) by Jeffrey S. Levinton

Surface seawater salinity

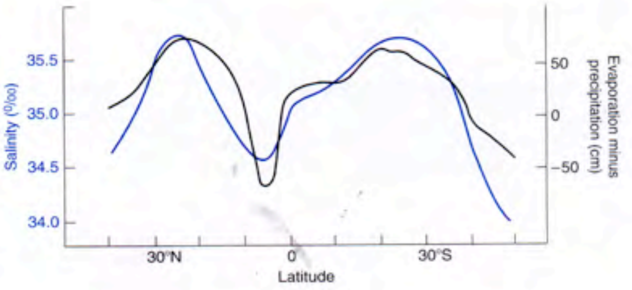
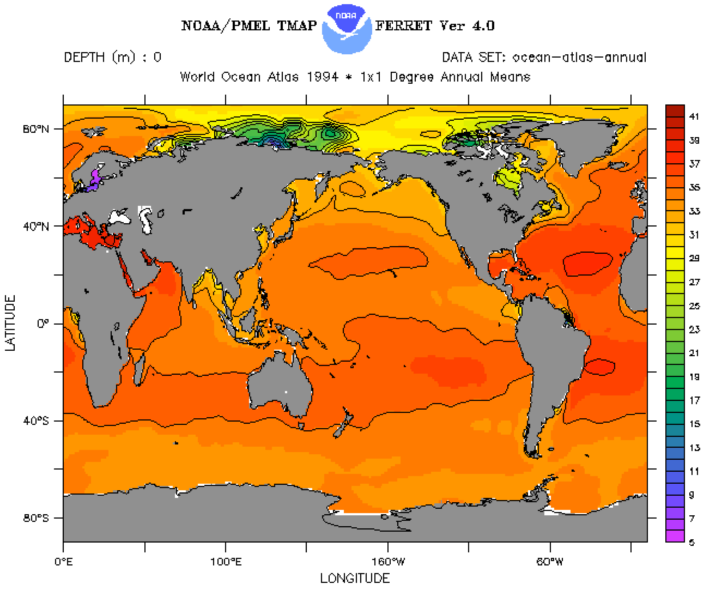


Fig. 2.8 Latitudinal variation in surface salinity of the open oceans (green curve). Balance of evaporation and precipitation also shown (black curve). (After Sverdrup et al., 1942.)



Salinity (psu)

www.windows.ucar.edu

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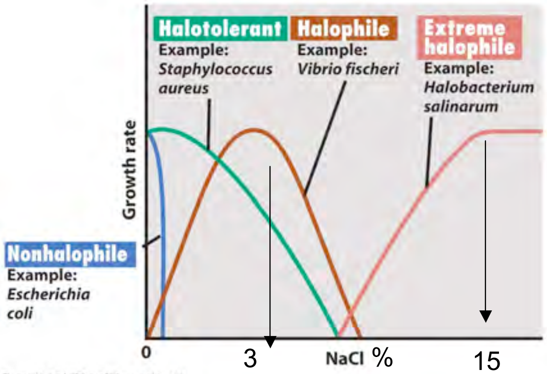
Water activity/Salt

- Cytoplasmic water activity must be maintained below that of that of the environment to promote osmotic influx of water to provide turgor pressure
- In low water activity environments, biologically compatible intracellular solutes must be imported or synthesized



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Salinity

- Narrow range in ocean; broad range in estuaries
- Na+ requirement in marine bacteria ("mild" halophiles)
- To grow in low water activity environments: obtain water by pumping ions in, or synthesize/concentrate an organic solute (non-inhibitory--compatible solutes; e.g. glycine betaine, glutamate, trehalose)
- Capacity to concentrate compatible solutes is genetically determined (and leads to adaptations to different salinity ranges)
- Survival of *E. coli* and *V. cholerae* in SW: Human health interest

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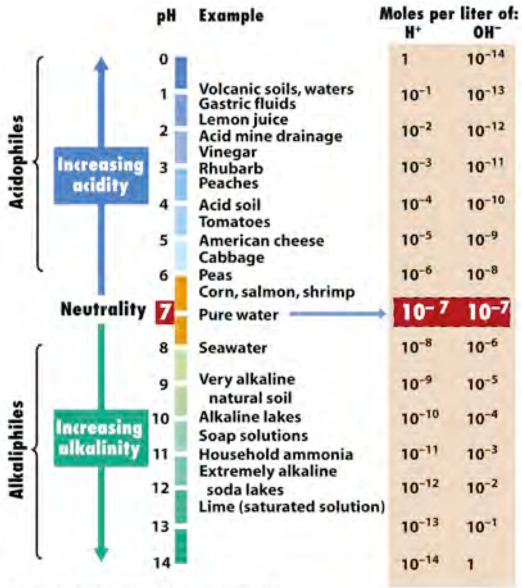
pH

- Most microbes have a pH growth range of 2-3 units
- Generally, cytoplasm is circumneutral
  - Exceptions exist 4.5-9
- Seawater is near pH 8
  - Fairly constant
  - Microhabitats with lower pH common
- Energy is required to maintain cytoplasmic pH



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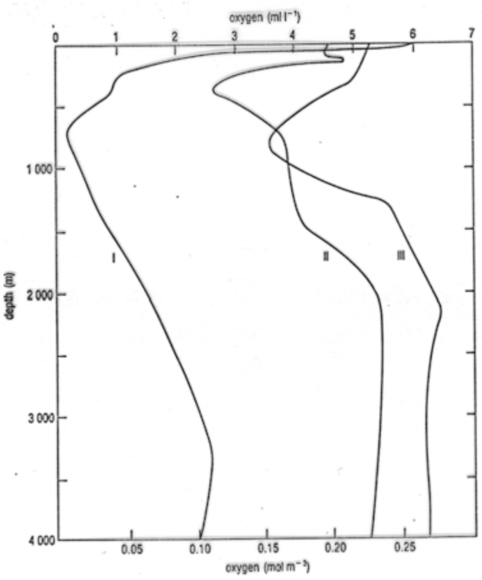
Oxygen as a Variable



O2 is poorly soluble in water, affected by temperature

I. S Cal

II. E South Atlantic

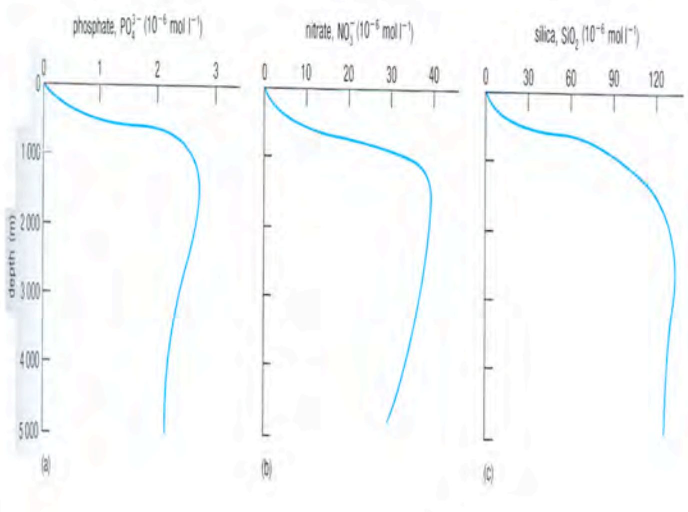
III. Gulf Stream

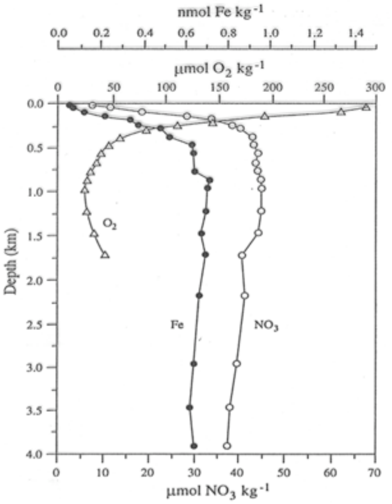
Open University. Seawater: Its composition, Properties and Behavior. 1991.

Oxygen as a Variable

- Absolute requirement only by **aerobes**
- **Microaerophiles** tolerate low levels of O_2
- **Facultative aerobes** are quite common; can grow under aerobic or anaerobic conditions
- **Anaerobes**: Strict (killed) or aerotolerant (can detoxify)
- Most ocean water column is oxygenated, although sub-saturated (esp. E. Tropical Pacific, N. Arabian Sea) but significant anoxic env. (Black Sea); sediments and suspended/sinking particles, guts of animals, etc. may be anoxic.

Inorganic Nutrient Profiles





Open University. Seawater: Its composition, Properties and Behavior. 1991.
Martin et al. 1989 Deep Sea Research 36:649-680

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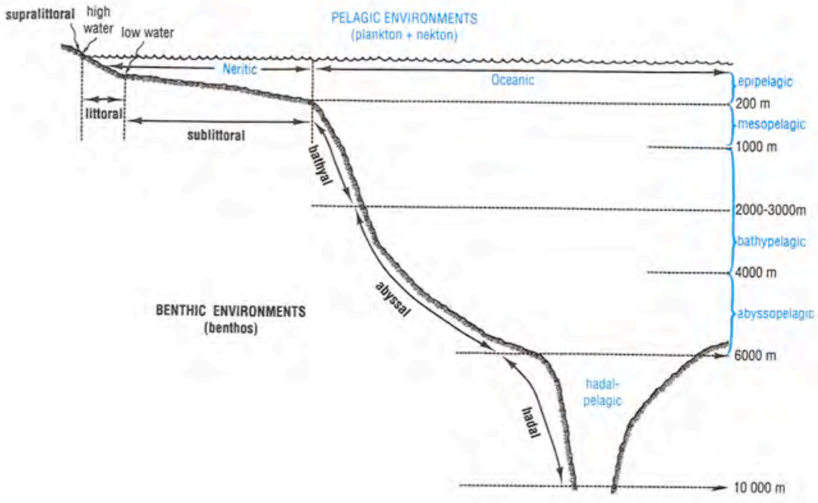
Microbial Habitats



Lalli & Parsons, 1997

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Scale of Microbial Environments

- Macroenvironments
- Microenvironments
- Gradients of environmental variables
- The importance of integrating across scales

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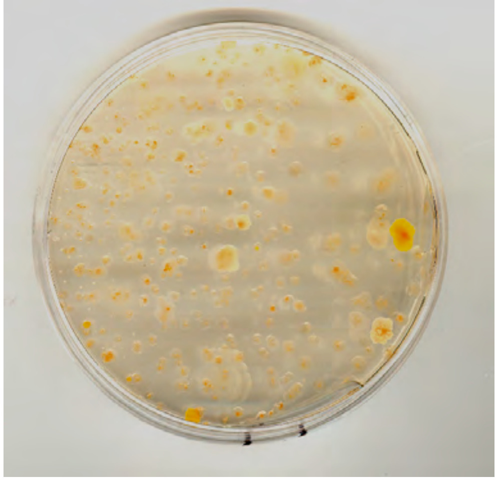
<1977: Bacteria considered unimportant in marine ecosystems



Low plate count- Typical cfu= 10^3 ml^{-1}

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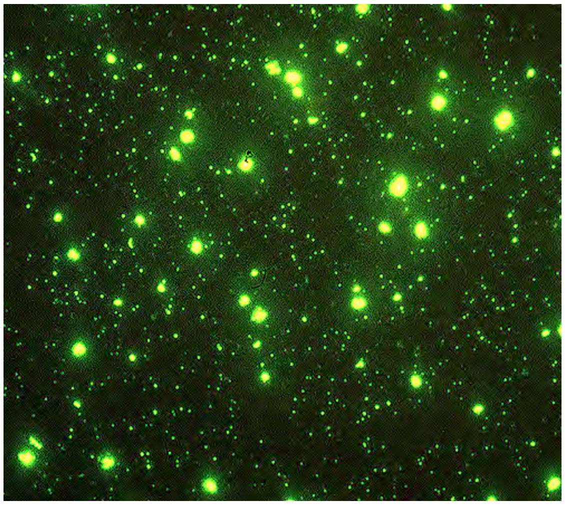
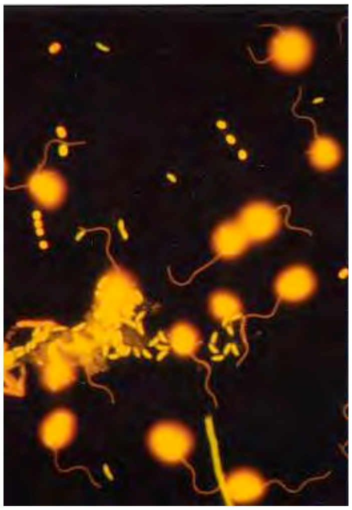
< 1 microliter of seawater under epifluorescence microscope (1000x)



Bacteria & viruses
Image from Noble lab



Protozoa
Image from Suzuki lab

- **We had missed >90% biomass, metabolism and biodiversity**

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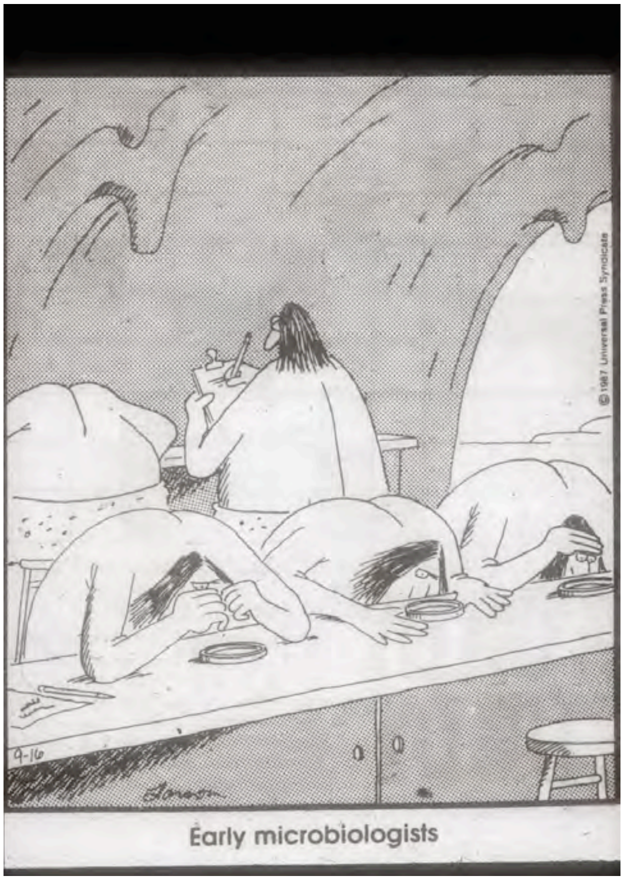

Early microbiologists

The Age of Discovery

- **1977 Bacteria 10^6 ml^{-1} (10^3 x cfu)**
- **'79-'80 High bacterial growth & C demand (dynamic populations)**
- **'84 Protozoa (10^3 ml^{-1}) major predators on bacteria**
- **'79-'90 Viruses abundant (10^7 ml^{-1}) & major predators on bacteria**
- **'79 *Synechococcus* 10^3 - 10^5 ml^{-1}**
- **'88 *Prochlorococcus* 10^4 - 10^5 ml^{-1}**
- **'92-'93 Widespread Archaea throughout the oceans (10^4 - 10^5 ml^{-1})**
- **'90s-today Rise of molecular ecology; marine genomics & proteomics; document diversity; culture the "unculturable"**

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Energy source	**electron donor**	**carbon source**
photo- (light)	litho- (inorganic)	auto- (CO_2)
chemo- (organic or inorganic chemicals)	organo- (organic)	hetero- (reduced organic)

- Combined with "-troph" the roots are used alone or in combination
  Examples:
    photolithoautotroph (photoautotroph)
    photolithoheterotroph (photoheterotroph)
    photoorganoheterotroph (photoorganotroph)
    chemolithoautotroph (chemoautotroph)
    chemolithoheterotroph
    chemoorganoheterotroph (or chemoheterotrophs or heterotroph)
  Missing:
    photoorganoautotroph
    chemoorganoautotroph
  Mostly will use the terms without specifying C source:
    photolithotroph
    photoorganotroph
    chemolithotroph
    chemoorganotroph
- **these terms are useful because they focus on chemical activities of organisms rather than classification based on species and genus**

- obligate vs facultative vs mixotrophic
- aerobic vs facultative anaerobe vs anaerobe
- electron acceptors

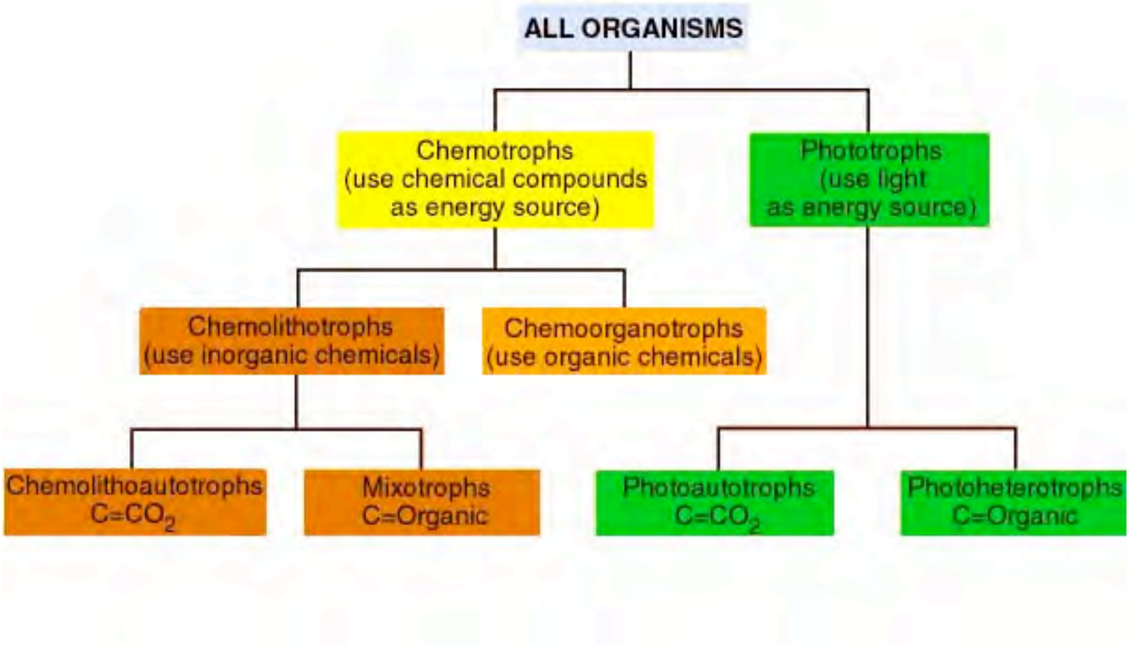
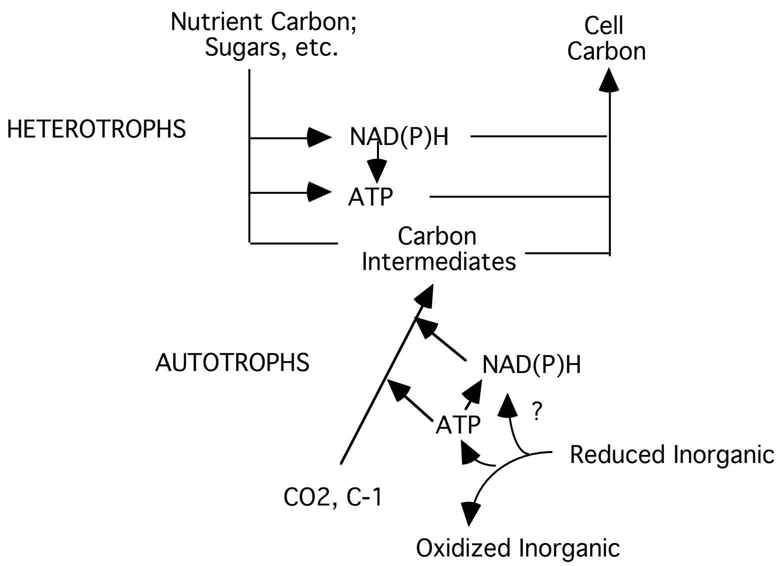


Fig. 15.1 in *Brock Biology of Microorganisms* (9th ed.)

Metabolic Diversity

Type	Electron Donor	Electron Acceptor	Carbon Source	Examples
Photolithotrophy	H_2O	CO_2	CO_2	plants, cyanobacteria (oxygenic photosynthesis)
	H_2S	CO_2	CO_2	purple sulfur bacteria (Chromatiaceae)
				green sulfur bacteria (Chlorobiaceae)
Photoorganotrophy	organics	organics	organics	purple nonsulfur bacteria (Rhodospirillaceae)
Chemoorganotrophy	organics	O_2	organics	aerobic heterotrophs (pseudomonads)
	organics	NO_3^-	organics	denitrifiers (pseudomonads)
	organics	$SO_4^=$	organics	sulfate reducers (*Desulfovibrio)*
	organics	Fe^{3+} , MnO_2	organics	iron and manganese reducers
	organics	organics	organics	fermenters (*Clostridia*)
Chemolithotrophy	H_2	O_2	CO_2	hydrogen-oxidizing bacteria
	H_2S, S^0, SSO_3^-	O_2	CO_2	sulfur oxidizing bacteria (thiobacilli)
	H_2S	NO_3^-	CO_2	anaerobic sulfur oxidizing bacteria
				(Thiobacillus denitrificans)
	Fe^{2+}	O_2	CO_2	Iron oxidizing bacteria (*Th. ferrooxidans)*
	NH_3	O_2	CO_2	Ammonia oxidizing bacteria (Nitrifiers) (*Nitrosomonas*)
	NO_2^-	O_2	CO_2	Nitrite oxidizing bacteria (Nitrifiers) (*Nitrobacter*)
	CH_4, CH_3OH	O_2	CO_2, HCOH	Methanotrophs and methylotrophs
	H_2	$SO_4^=$	CO_2	Sulfate reducing bacteria (some)
	H_2	CO_2	CO_2	Methanogens
	H_2	CO_2	CO_2	Acetogens

Overview of Cell Metabolism



Nutrient Carbon;
Sugars, etc.

Cell
Carbon

HETEROTROPHS

NAD(P)H

ATP

Carbon
Intermediates

AUTOTROPHS

NAD(P)H

ATP

?

Reduced Inorganic

CO2, C-1

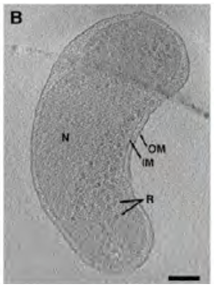
Oxidized Inorganic

Major players

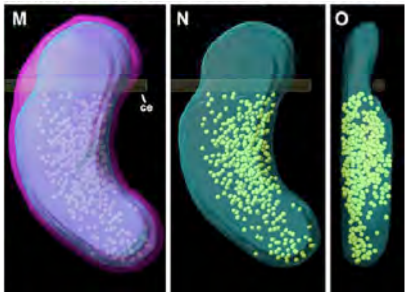
- Bacteria
  - Cyanobacteria ex. *Synechococcus*, *Prochlorococcus*: oxygenic photoautotrophs
  - Alpha proteobacteria, ex. *Candidatus* Pelagibacter ubique: chemoorganotrophs
- Archaea
  - Mesophilic marine crenarchaeota, ex. *Nitrosopumilis maritima*: chemolithoautotrophs*?*

Pelagibacter ubique

- Chemoorganoheterotroph
- Highly abundant (25%), pelagic
- Adapted to oligotrophy
- Slow growing, never reach high cell density, grow only in seawater
- Non-motile
- Auxotrophic for glycine and serine
- Requires vitamins and reduced sulfur (DMSP)
- Lacks conventional stationary phase
- Makes proteorhodopsin



100 nm



Nicastro et al.. Microsc
Microanal (2006) vol.
12(Supp 2) p. 180

Ca. P. ubique genome is tiny

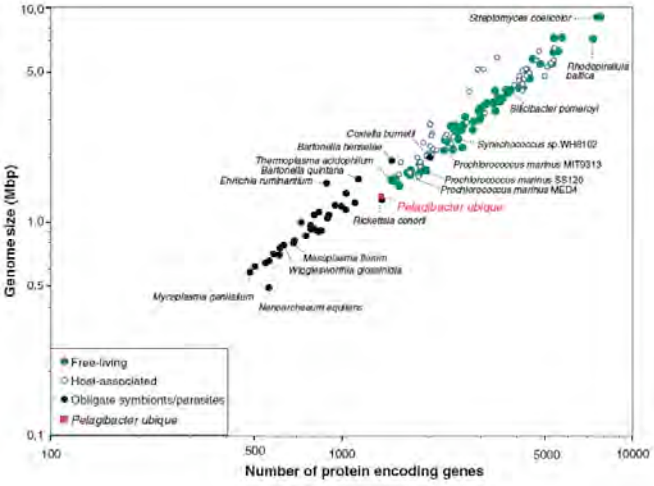
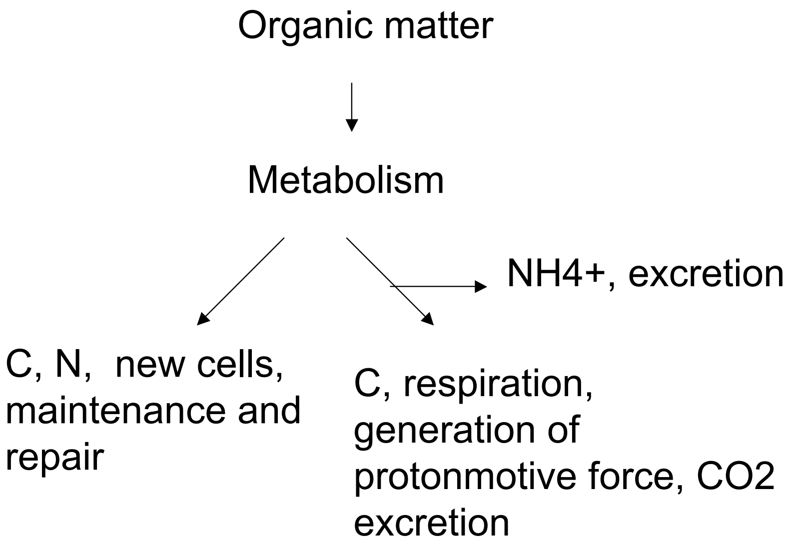


Fig. 1. Number of predicted protein-encoding genes versus genome size for 244 complete published genomes from bacteria and archaea. *P. ubique* has the smallest number of genes (1354 open reading frames) for any free-living organism.

Heterotrophic metabolism



Organic matter

Metabolism

NH4+, excretion

C, N, new cells, maintenance and repair

C, respiration, generation of protonmotive force, CO2 excretion

Bacteriorhodopsin (similar to proteorhodopsin)

- Light-driven proton pump
  - Light drives the retinal chromophore from relaxed trans to energetic cis form (like loading a spring)
  - Energy is released so that a proton is transported out of the cell
- Used for:
  - ATP synthesis
  - Transport
- Allows survival when no organic energy sources are available
- Unlike photosynthesis, does *not* provide reducing power for C fixation or biosynthesis

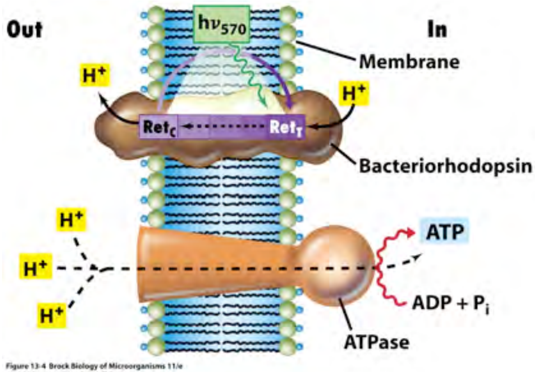


Figure 13-4 Brock Biology of Microorganisms 11/e
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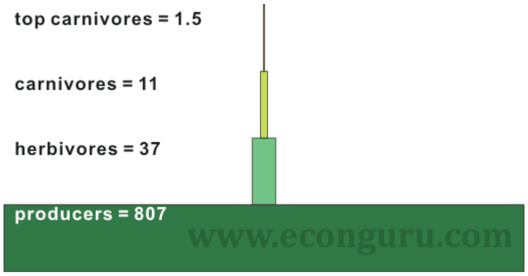
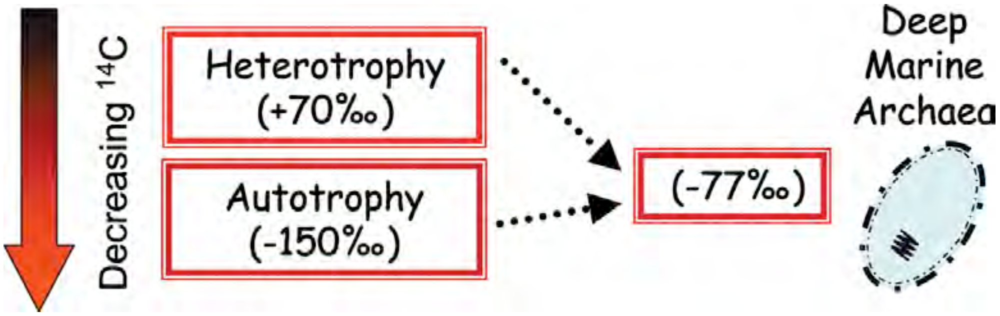
Proteorhodopsin

- Cells can be more efficient under C limited conditions, less loss to respiration
- Survive starvation



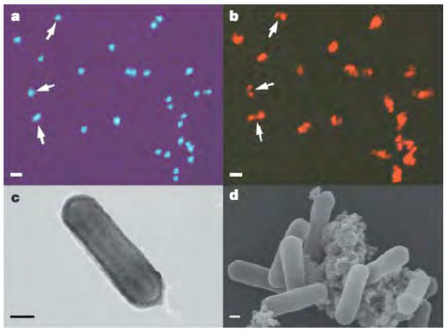
Marine archaea rely mainly on autotrophic metabolism. They comprise up to 40% of cells in deep ocean water

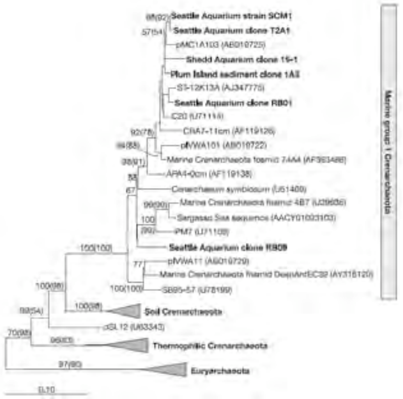


PNAS 2006;103:6413-6414

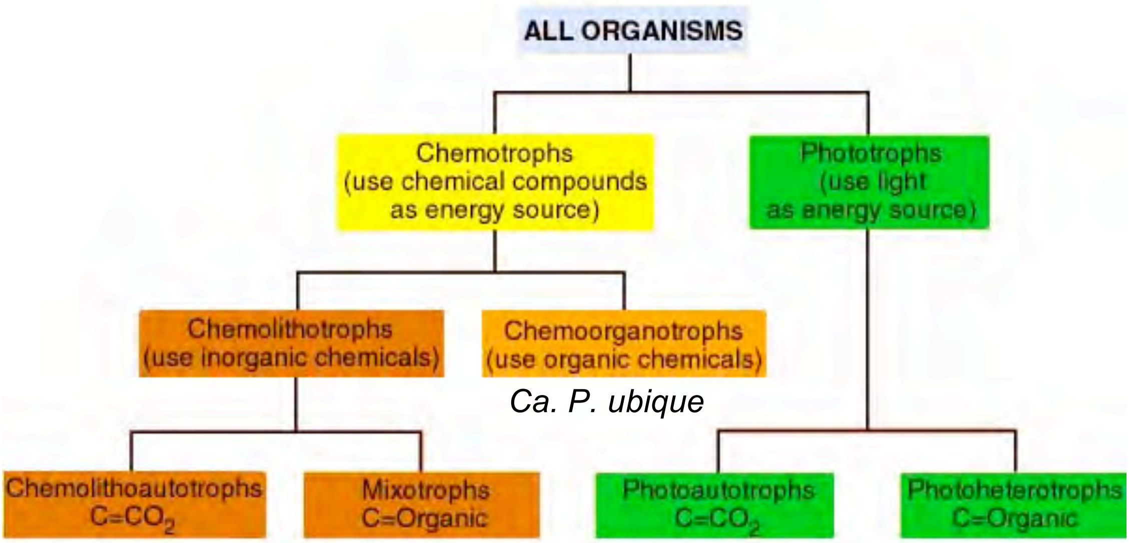
Nitrosopumilis maritimus

- Only cultivated member of the marine crenarchaeota
- Isolated from aquarium gravel
- Chemolithoautotroph: ammonia oxidation





Konneke et al. Nature (2005) vol. 437 pp. 543-546



Ca. P. ubique

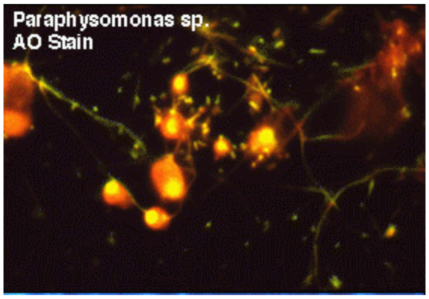
N. maritimus

cyanobacteria

Ca. P. ubique

Fig. 15.1 in *Brock Biology of Microorganisms* (9th ed.)

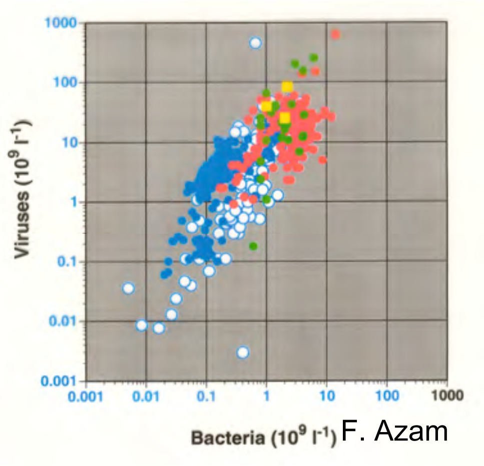
Predation on bacteria



Flagellates
- 2-5 μm in diameter
- abundance: 10^3 mL^{-1}
- graze ~ 50% of bacterial production

Viruses
- 20-250 nm in diameter
- 10^7-10^8 mL^{-1}
- species-specific predators
- kill ~ 50% of bacterial population
- “futile cycle” of C flow

Metazoan
- specialized mucus-net feeders
- ingestion of bacteria attached to particles



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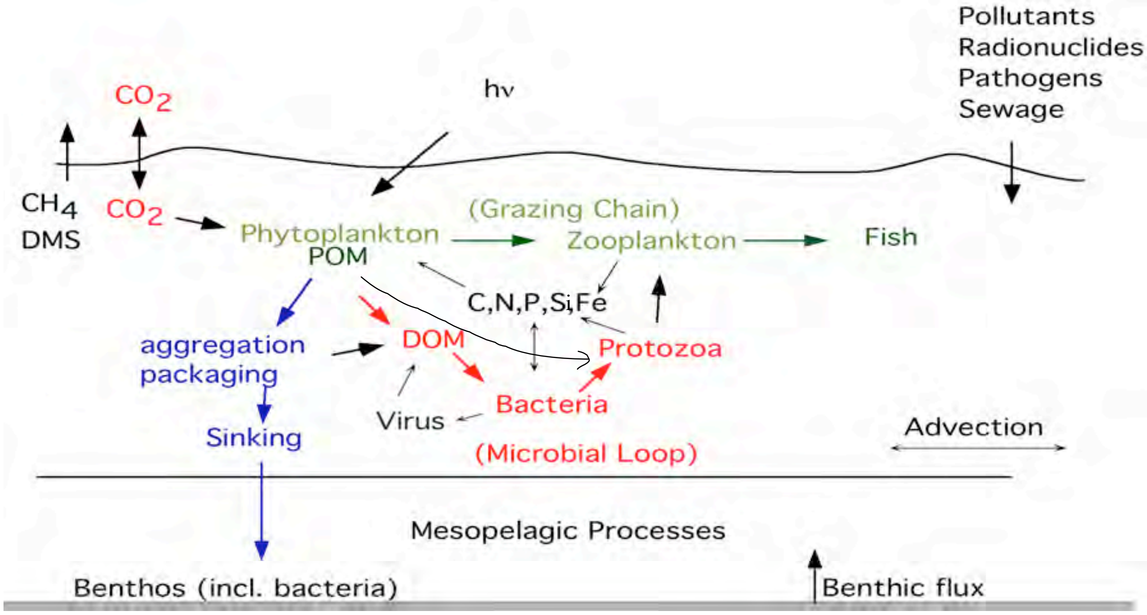
Heterotrophic bacteria

- Recognized to play a key role in the carbon cycle
- Consume dissolved organic matter (DOM) converting it to particulate organic matter (cells, POM) and CO2 (respiration)
- Also convert POM to DOM, bacterial cells and CO2

Microbes in marine ecosystems: Integrative View



- -> C flux into bacteria a major variable pathway; affects biogeochem variability
- How do we integrate bacterial processes into ecosystem models?
-

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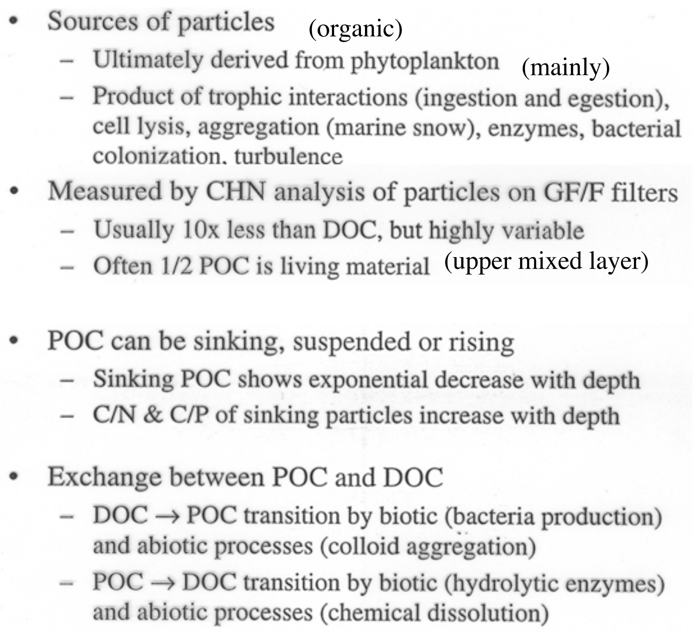
Particulate organic matter



- Sources of particles (organic)
  - Ultimately derived from phytoplankton (mainly)
  - Product of trophic interactions (ingestion and egestion), cell lysis, aggregation (marine snow), enzymes, bacterial colonization, turbulence
- Measured by CHN analysis of particles on GF/F filters
  - Usually 10x less than DOC, but highly variable
  - Often 1/2 POC is living material (upper mixed layer)
- POC can be sinking, suspended or rising
  - Sinking POC shows exponential decrease with depth
  - C/N & C/P of sinking particles increase with depth
- Exchange between POC and DOC
  - DOC → POC transition by biotic (bacteria production) and abiotic processes (colloid aggregation)
  - POC → DOC transition by biotic (hydrolytic enzymes) and abiotic processes (chemical dissolution)

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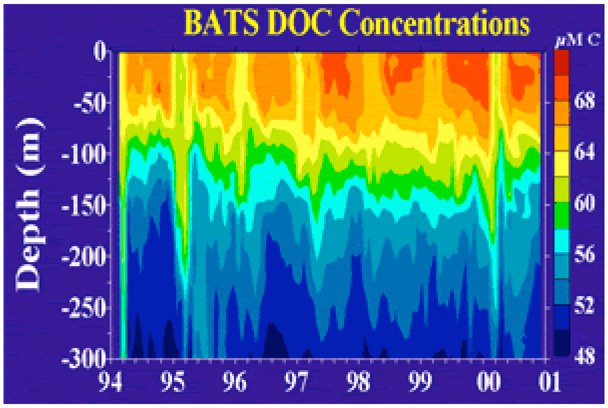
Seasonal and annual variability of DOC in the water column: Sargasso Sea



Carlson web page

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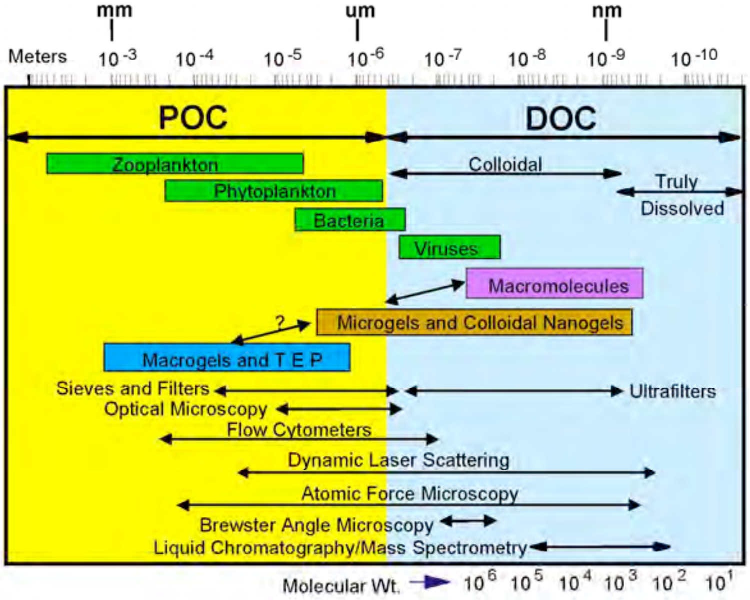
A unifying context for bacteria-OM interactions

➢Bacterial environment is an OM continuum



Verdugo et al., Mar. Chem.

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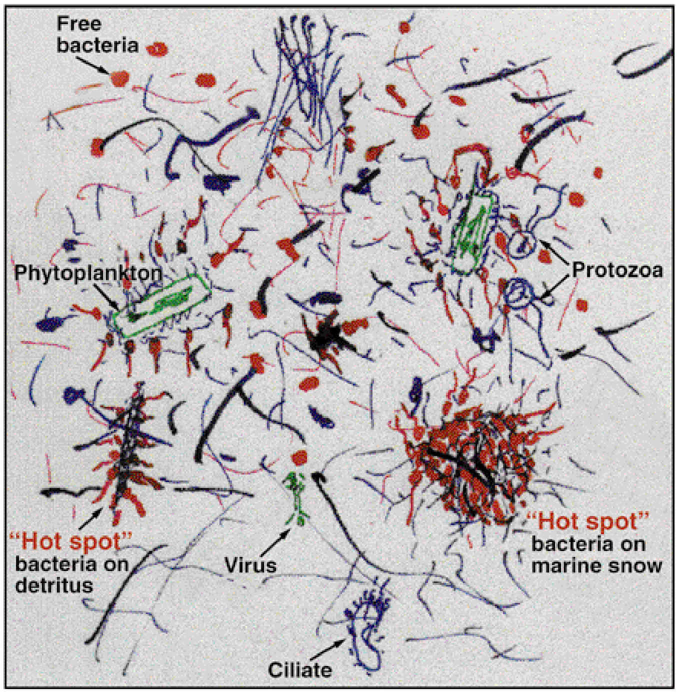
Micro-scale heterogeneity and µ-environment structure
Context for bacterial structuring of ecosystem



Azam, F. 1998 Science 280:694-696

- **Implications for diversity, C cycling, nutrient-growth relations & microbial ecology**

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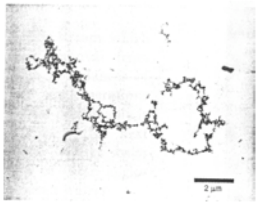
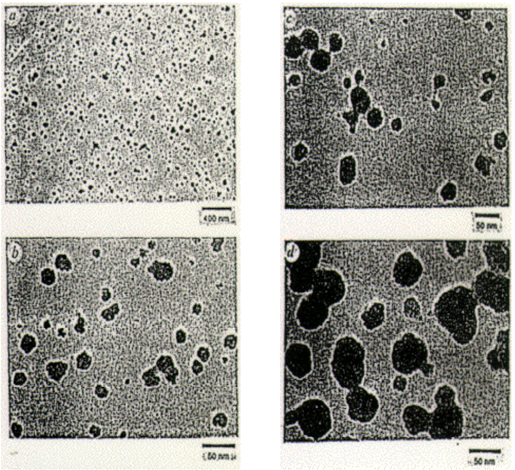
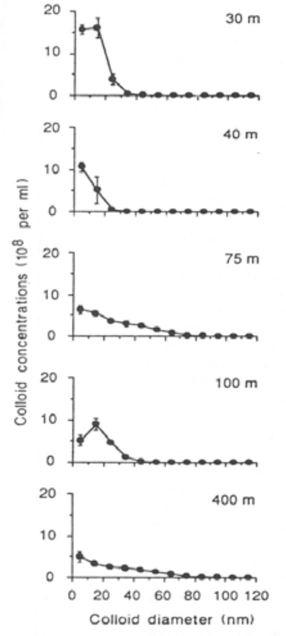
Colloids







- ~ 5 - 100 nm
- 10^8-10^9 ml^{-1}

Wells & Goldberg 1991. Nature. 353: 342-344.

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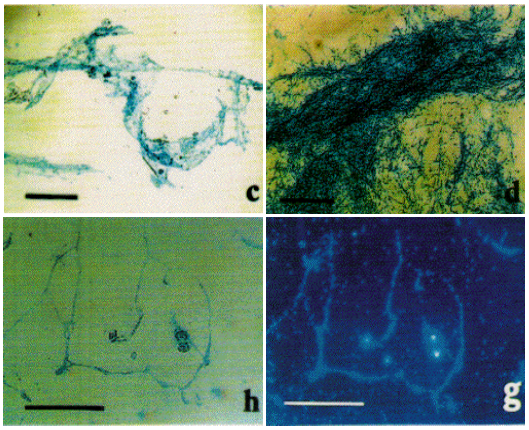
Transparent Exopolymer Particles (TEP)



- ~ 10^3 ml^{-1}: 2-100s µm; many colonized

Alldredge *et al.* 1993. Deep-Sea Res.40: 1131-1140.

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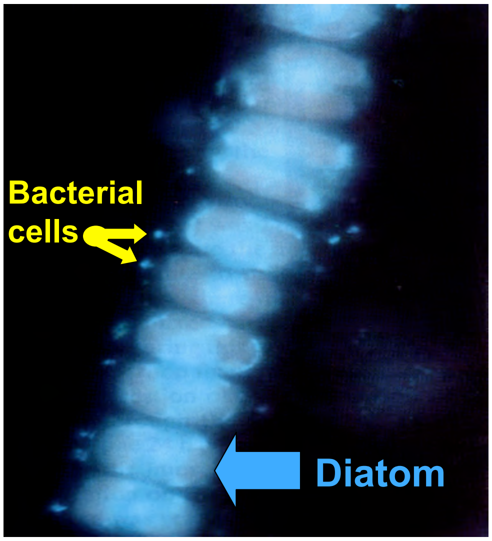
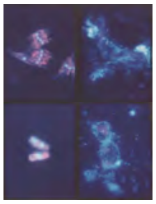
nm-µm scale bacteria-phytoplankton interactions have ecosystem scale C cycle consequences



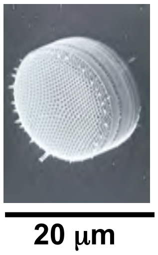
- **Bacteria interact w/ phytoplankton as part of OM continuum**
- **Create N, P, Fe hot-spots sustaining rapid primary production**
- **Enzymes reduce diatom ‘stickiness’, inhibit aggregation and sinking**
- **DMSP--> DMS kinetics enhanced**

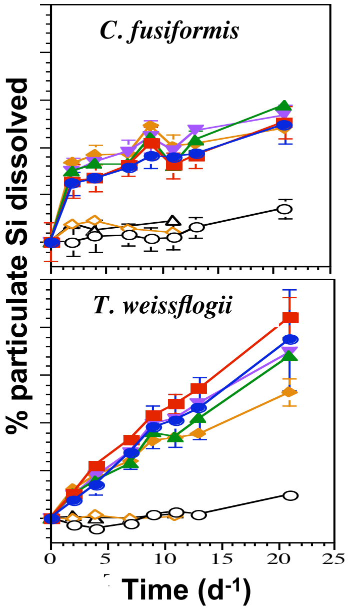
F. Azam

Smith, Steward, Long & Azam.1995. Deep-Sea Res. 42: 75-97
Cantin, Levasseur, Schultes, Michaud. 1999. AME 19:307-312



Nanometer scale action of bacteria regulates global ocean Si (and C) cycles





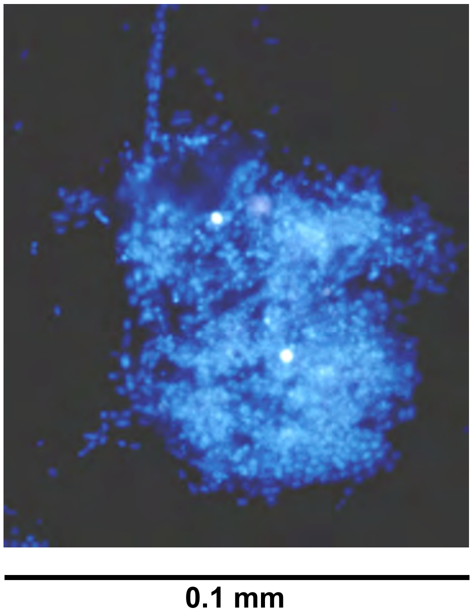
- Colonizer proteases hydrolyse protective matrix, cause rapid silica dissolution
- Variables: Species; colonization and *hydrolase intensity*; temperature
- µ-scale enzyme action affects Ocean basin Si and C cycles

Bidle & Azam.1999. Nature 397: 508-512

Bidle, Manganelli and Azam. 2002. Science 298:1980-1983

F. Azam

Microscale biochemistry structures ocean ecosystems: bacterial carbon cycling on marine snow

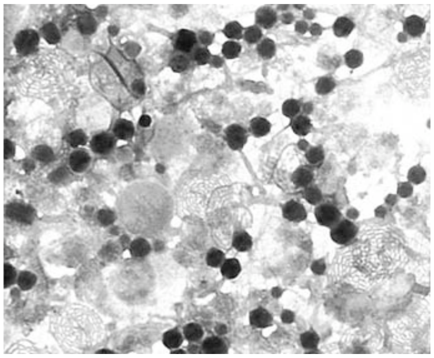


- Leaves DOM plume in its wake
- High cell density 10^7-10^{10} ml^{-1}
- Nutrients, energy (& pollutants?) retained in upper ocean
- Enzymatic control of energy flux to the deep sea
- Rapid hydrolysis but low uptake

Smith, Simon, Alldredge & Azam. 1992. Nature 359: 139-142
Azam & Long. 2001. Nature 414:496-498

F. Azam

Marine bacteriophages



- •Most common predator in the ocean
  - ~10^7 phage ml-1
- • Major players in global C cycling
  - - increase respiration
  - - decrease primary production
- • Transduction and lysogenic conversion - increase genetic malleability
- • Increase microbial diversity
- - “kill the winner”

Article discussion

Phases of growth in batch culture

- lag phase (adaptation to new conditions)
- logarithmic phase (maximal, characteristic rate for the particular conditions = balanced growth)
- stationary phase (cessation of growth upon exhaustion of nutrients or accumulation of inhibitory end products, adaptation for dispersal)

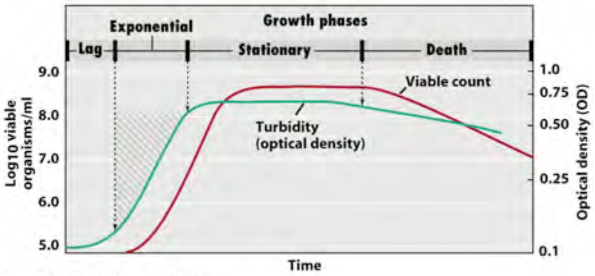


Figure 6-8 Brock Biology of Microorganisms 11/e
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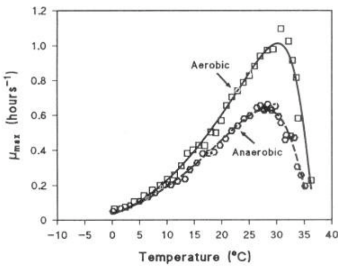
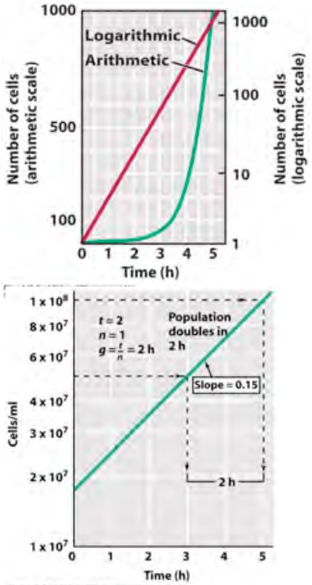
Growth terms

- All of these are based on balanced growth (all nutrients in excess)
- growth rate, cells/time = dN/dt=kN,
  - k (also called μ)=growth rate constant, in units of time^{-1}, (usually h). in many studies of growth rate, k (μ) is measured, then plotted as a function of something like temperature
    - N is the concentration of cells (#/volume, population density)
- generation time = doubling time = g = ln2/k = 0.693/k
  - the inverse of doubling time, 1/g often used, this gives doublings per hour (this is called μ in Neihardt, and ν in Brock,)



Growth data

- $\log_{10}N - \log_{10}N_0 = k(t-t_0)/2.303$,
  - consequently plotting the $\log_{10}$ of cell number or mass vs time gives a straight line with slope of k/2.303,
  - semilog plots are most common for study of growth of cells in batch culture
- linear (arithmetic) growth will occur if growth is limited by something provided at a constant rate, such as oxygen



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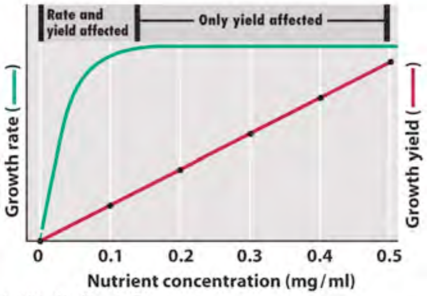
Growth Yield

- growth yield, Y is a measure of efficiency
  - $X - X_0 = YC$, C is the initial concentration of the limiting nutrient (X=cell mass)

Nutrient limitation

- Growth rate as a function of nutrient concentration
  - $k = k_{max} * C/(Ks + C)$
  - Michaelis-Menten type kinetics,
    - Ks is analogous to the MM constant Km,
    - for glucose in E. coli Ks is µmolar, much less than normally used in culture media.
    - kmax is the maximum growth rate under the particular conditions.



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Properties of Nitrogen

- Nitrogen is a major nutrient required by all cells
- Redfield ratio N:P=16:1
- Common species and oxidation states (cast of characters)
  - NH_4^+, -3: This is the oxidation state in proteins. NH_4- is the source of N in amino acid biosynthesis, ammonium
  - NH_2OH, -1, hydroxylamine
  - N_2, 0, Major form in the atmosphere, past and present, very unreactive species, nitrogen gas
  - N_2O, +1, gaseous, nitrous oxide
  - NO , +2, gaseous, nitric oxide
  - NO_2^-, +3, nitrite
  - NO_3^-, +5, nitrate

The modern N cycle

- Yellow is oxidation
- Red is reduction
- White is no redox change
- The full range of species is present

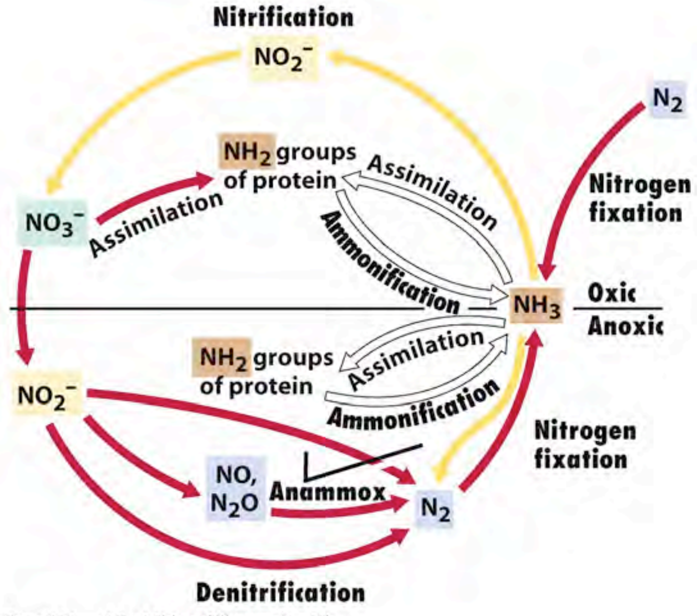

Figure 19-28 part 2 Brock Biology of Microorganisms 11/e
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The History of Nitrogen

- Until the rise of O_2 due to oxygenic photosynthesis about 1 bya, N_2 and NH_4^+ were the dominant species
- NH_4^+ relatively abundant from geological sources
- Consistent with high levels of N in organisms
- Consistent with NH_4^+ as fundamental source of N in cells - simplest assimilation
- Thus during most of biological evolution, N was not a problem

The ancient N cycle in an anoxic world

- No redox cycling
- N2 fixation not needed (?)

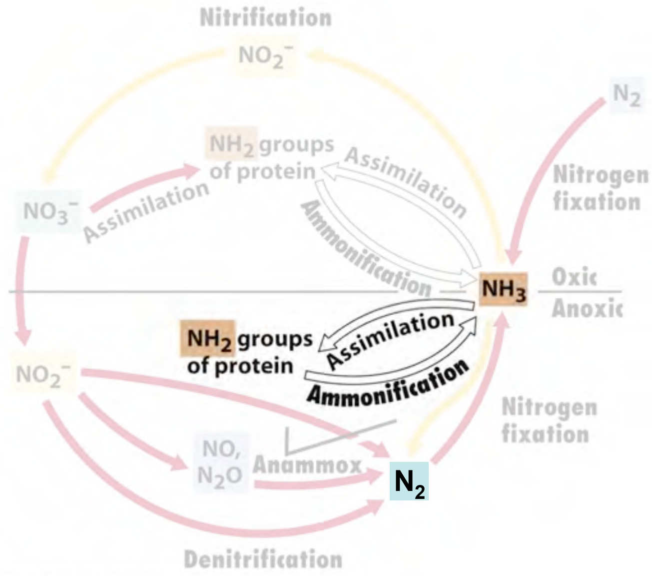

Figure 19-28 part 2 Brock Biology of Microorganisms 11/e
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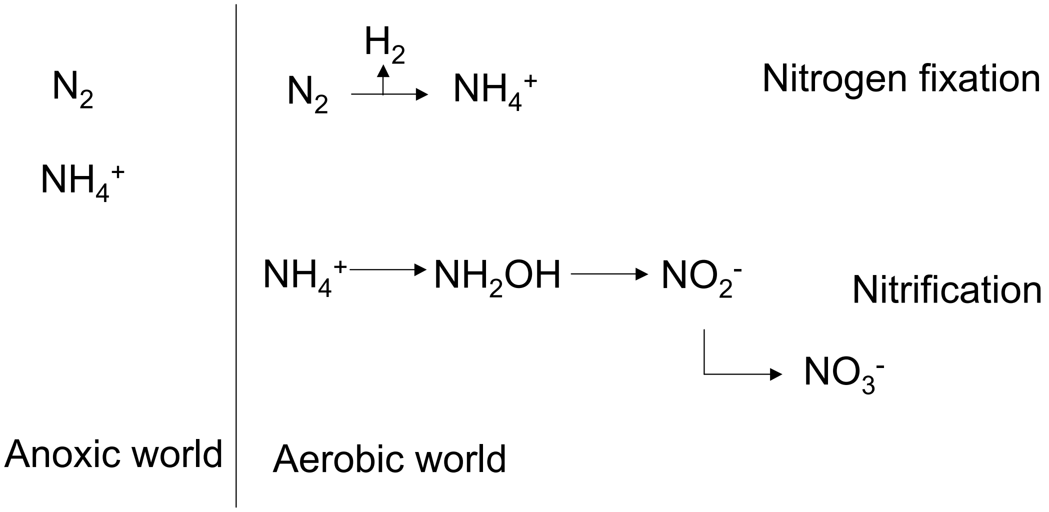
The History of Nitrogen, II

- The oxygenation of the atmosphere precipitated a nitrogen crisis
- Free O_2 would react with ammonia to produce N_2 and various nitrogen oxides, reducing N availability and creating selective pressure for N_2 fixation
- This situation also presents an opportunity for lithoautotrophs that can grow using reduced N as an electron donor and O_2 as an electron acceptor

Processes evolving in response to NH_4^+ oxidation after the appearance of oxygen



N_2

NH_4^+

$N_2 \xrightarrow{H_2} NH_4^+$ Nitrogen fixation

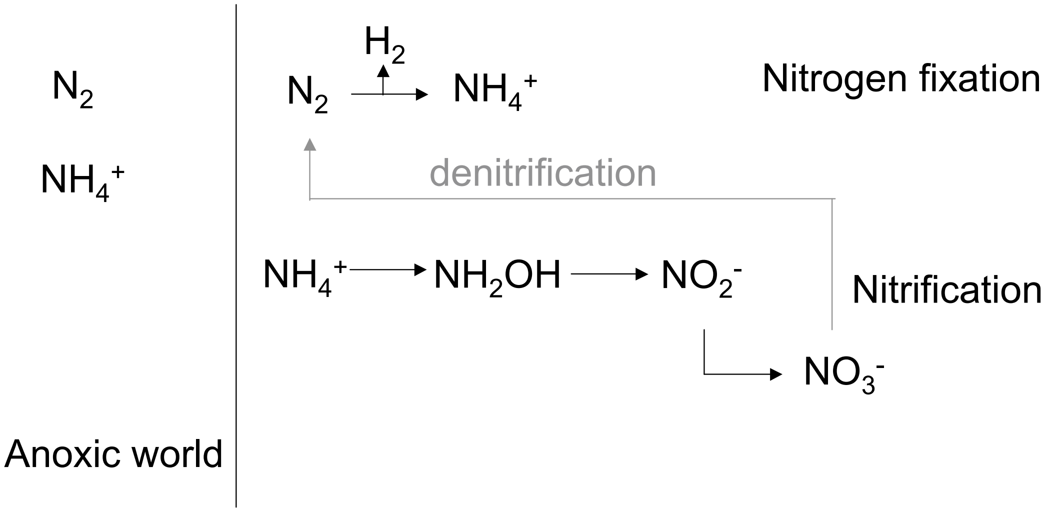
$NH_4^+ \rightarrow NH_2OH \rightarrow NO_2^-$ Nitrification

$\rightarrow NO_3^-$

Anoxic world

Aerobic world

Processes evolving in response to NH_4^+ oxidation after the appearance of oxygen



N_2

NH_4^+

$N_2 \xrightarrow{H_2} NH_4^+$ Nitrogen fixation

denitrification

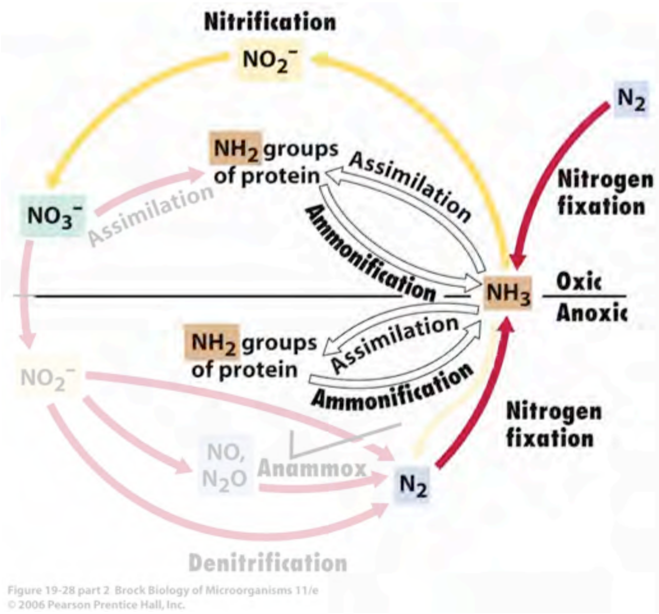
$NH_4^+ \rightarrow NH_2OH \rightarrow NO_2^-$ Nitrification

$\rightarrow NO_3^-$

Anoxic world

N cycle in the early aerobic world

- Nitrogen fixation compensates for oxidative loss of NH_4^+
- Lithoautotrophic oxidation of NH_4^+ by oxygen occupies a new niche



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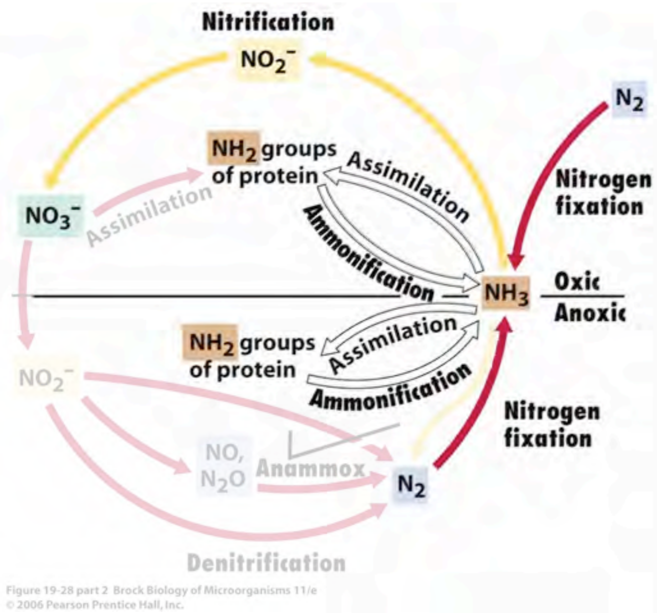
Conventional nitrification: old but not ancient?

- No organism known to take NH_4^+ all the way to NO_3^-
- NH_4^+–>NO_2^-
  - Bacteria (*Nitrosomonas*), archaea
- NO_2^- –> NO_3^-
  - Bacteria (*Nitrobacter*)
- Both require oxygen
- Both support autotrophy



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Nitrification, a lousy way to make a living

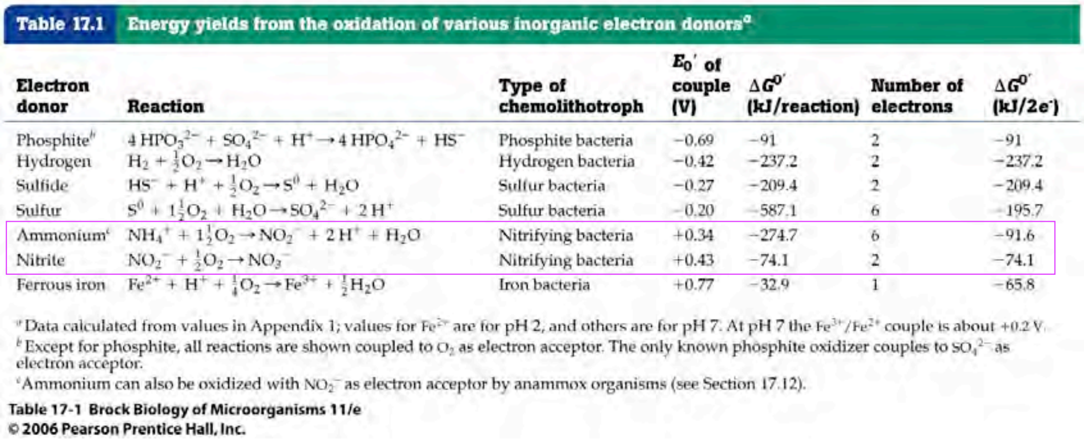

Table 17.1 Energy yields from the oxidation of various inorganic electron donors[a]

Electron donor	Reaction	Type of chemolithotroph	E_0' of couple (V)	$\Delta G^{0'}$ (kJ/reaction)	Number of electrons	$\Delta G^{0'}$ (kJ/2e⁻)
Phosphite[b]	$4\,HPO_3^{2-} + SO_4^{2-} + H^+ \rightarrow 4\,HPO_4^{2-} + HS^-$	Phosphite bacteria	−0.69	−91	2	−91
Hydrogen	$H_2 + \frac{1}{2}O_2 \rightarrow H_2O$	Hydrogen bacteria	−0.42	−237.2	2	−237.2
Sulfide	$HS^- + H^+ + \frac{1}{2}O_2 \rightarrow S^0 + H_2O$	Sulfur bacteria	−0.27	−209.4	2	−209.4
Sulfur	$S^0 + 1\frac{1}{2}O_2 + H_2O \rightarrow SO_4^{2-} + 2\,H^+$	Sulfur bacteria	−0.20	−587.1	6	−195.7
Ammonium[c]	$NH_4^+ + 1\frac{1}{2}O_2 \rightarrow NO_2^- + 2\,H^+ + H_2O$	Nitrifying bacteria	+0.34	−274.7	6	−91.6
Nitrite	$NO_2^- + \frac{1}{2}O_2 \rightarrow NO_3^-$	Nitrifying bacteria	+0.43	−74.1	2	−74.1
Ferrous iron	$Fe^{2+} + H^+ + \frac{1}{4}O_2 \rightarrow Fe^{3+} + \frac{1}{2}H_2O$	Iron bacteria	+0.77	−32.9	1	−65.8

[a] Data calculated from values in Appendix 1; values for Fe^{2+} are for pH 2, and others are for pH 7. At pH 7 the Fe^{3+}/Fe^{2+} couple is about +0.2 V.

[b] Except for phosphite, all reactions are shown coupled to O_2 as electron acceptor. The only known phosphite oxidizer couples to SO_4^{2-} as electron acceptor.

[c] Ammonium can also be oxidized with NO_2^- as electron acceptor by anammox organisms (see Section 17.12).

Table 17-1 Brock Biology of Microorganisms 11/e

Nitroso-, NH_4^+ –> NO_2^-

- Two enzymes involved:
  - Ammonia monooxygenase, a membrane protein
  - Hydoxylamine oxidase, a periplasmic enzyme

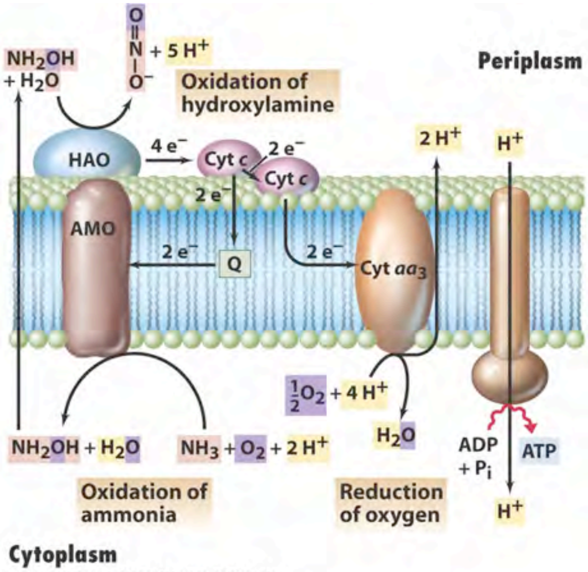

Figure 17-32 Brock Biology of Microorganisms 11/e